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SOME ASPECTS OF THE COMPARATIVE ECOLOGY OF POPULATIONS OF THE FOUR *PATROBUS* SPECIES (COLEOPTERA : CARABIDAE : PATROBINI) AT GEORGE LAKE, ALBERTA

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Some aspects of the comparative ecology of populations of the four *Patrobus* species (Coleoptera : Carabidae : Patrobini) at George Lake, Alberta," submitted by Alan Carter in partial fulfilment of the requirements for the degree of Master of Science.

Abstract

Some ecological characters of adults and larvae of four carabid species were studied at George Lake, Alberta, during 1968 and 1969. The characters were habitat preferences, seasonal activity and distribution patterns, daily activity rhythms, oviposition sites, and overwintering stages. The species were: *Patrobus stygicus* Chaudoir, *P. lecontei* Chaudoir, *P. foveocollis* Eschscholtz, and *P. septentrionis* Dejean. The other North American species, *P. longicornis* Say and *P. fossifrons* Esch were compared with the George Lake species. *Patrobus stygicus*, *P. foveocollis* and *P. septentrionis* overwintered as larvae and adults. *Patrobus lecontei* overwintered only as larvae.

Larvae and adults of *P. foveocollis* were least hygrophilous and ranged from forest clearings through forest margins, sedge meadows, to *Salix* habitats, adjoining the marshes. Larvae and adults of *P. stygicus* were most hygrophilous and extended from forest margin through shallow marsh to the lakeside. *Patrobus lecontei* larvae and adults extended from forest margin to shallow marsh. Adults of *P. septentrionis* occurred mostly in sedge meadows, and their larvae were not found. Individuals of this species were rare in comparison with those of the other *Patrobus* species at George Lake. The ranges of spatial distribution of the carabids were greatest during their main periods of activity between May and September, and September and November for adults and larvae respectively. The ranges were least prior to and just after overwintering, their periods of low activity. During the latter periods the carabids tended to aggregate

together in drier habitats.

Some aspects of the comparative ecology of the four *Patrobus* species at George Lake are discussed under taxonomic characters, habitat occupation and life history features. Of the latter, adults of *P. lecontei* were characterized by rapid development of sexual maturity and short life, while adults of *P. stygicus* had a longer adult pre-reproductive period and longer life. The possible evolutionary significance of life history features and their consequences are discussed for the six North American *Patrobus* species.

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1. Introduction

Little of the natural history of the majority of North American carabids is yet known (Ball, 1960). In contrast the natural history and taxonomy of many European carabids is well known, and a number of laboratory and field studies have been done. Lindroth (1949) and Krogerus (1948) made extensive laboratory studies of preferenda and determined factors which lead to differential habitat selection of different species. Lindroth (1949) also combined a microclimatic and laboratory study and investigated factors that influenced the distribution of some closely related carabids of chalk grassland. More recent studies of preferenda (e.g. Thiele, 1964; Paarmann, 1966) and a number of comparative ecology ones followed. Of these latter, that of Van der Drift (1951) was one of the first. He sampled beech forest carabids mainly by pitfall trapping. Grüm (1962) and Greenslade (1964) used pitfall trapping with mark and recapture to study populations of some forest carabids.

However no worker has made an intensive study of the comparative ecology of a group of closely related carabid species, for example from the same subgenus, in an attempt to define ecological and behavioural characters which are useful in taxonomy and phylogeny.

Some aspects of the comparative ecology of populations of a group of fairly closely related carabids which frequent wet boreal habitats are considered. These populations live in the

vicinity of George Lake, Alberta and are of *Patrobus stygicus* Chaud., *P. lecontei* Chaud., *P. septentrionis* Dej., and *P. foveocollis* Esch.

The lack of comparative studies of carabids of wet habitats is in part due to sampling difficulties (Murdoch, 1966*a*) and to the poor state of the taxonomy of larvae of many genera (Lindroth, 1969). This is exemplified by the poor state of knowledge of populations of *Patrobus* species. Darlington (1938) and Lindroth (1961) included ecological notes on the six North American species in their taxonomic papers, but the biology of none of these species is known in detail. Only one of these species, *P. septentrionis*, is holarctic in distribution. Larsson (1939) and Murdoch (1967) summarized data about the life histories of the Palearctic *P. septentrionis* and *P. atrorufus* Stroem, and Larsson (1959) did likewise for the Icelandic form of *P. septentrionis*. Thiele (1964) studied factors which affected the distribution of larvae and adults of German *P. atrorufus*, mainly by a laboratory study.

The objectives of this study were to define ecological characters which are useful in taxonomic and phylogenetic studies of closely related species and to determine how closely related species use the resources of a restricted area. To achieve this, the local distribution of populations of *Patrobus* species at George Lake were compared with respect to life history and habitats, to determine the extent to which the distributions of these species were contiguous (rather than overlapping) in space and time.

The following questions were posed.

(1) Are local populations of different species that occur in the same general habitats, separated by seasonal activity?

(2) If not, are they separated in space during their period of main activity?

(3) Does the spatial distribution of carabids vary according to time of year?

Life history features were considered as adaptations (Cole, 1954). The evolutionary interpretation of these features and other ecological characters are based mainly on Darlington's (1938) hypotheses about the relationships of these species (see 8.) with the exception that *P. fossifrons* and *P. stygicus* are regarded as distinct species rather than subspecies (see Lindroth, 1961).

2. The field station and study areas

2.1. The field station

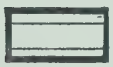
The field station is 53° 57'N and 114° 06'W about 40 miles northwest of Edmonton, Alberta. The area lies at the southern margin of the boreal mixed forest subzone (La Roi, 1968). Graham (1969) described the main vegetation zones. The land of the original square mile of property is marked off in grids of 100 metre^2 (Fig. 1). Study areas were located by station numbers which were designated by the grid reference of the SW corner of the quadrant(s) in which each study area occurred.

2.2. Main habitat types and study areas

For the purposes of this study it sufficed to classify wet habitats by indicator plant species and to note changes in water level within and between years (Elton and Miller, 1954). Wet habitats were divided into marsh and transition zones (Fig. 2).

Marshes. - Most of the marsh study areas were in the main marshes which adjoined the lake; one other, Marsh I, was isolated and surrounded by forest on all sides. There were two main habitat types in the marshes: (a) deep marsh was characterized by a floating mat of *Typha* specimens which extended from the lakeside to shallow marsh; this subzone corresponds with reed swamp as defined by Moss (1953, 1955); (b) shallow marsh which extended from deep marsh to *Salix* habitats in the transition zone. It consisted of tussocks of

Fig.1. George Lake field station showing wet habitats and study areas.



Wet habitats, transition and marsh zones.

Fire break. The fire of May 20,1968 was confined to the north of the field station.

Study areas. The station numbers of these study areas were designated by the grid reference of the S.W. corner of the quadrant(s) in which each occurred.

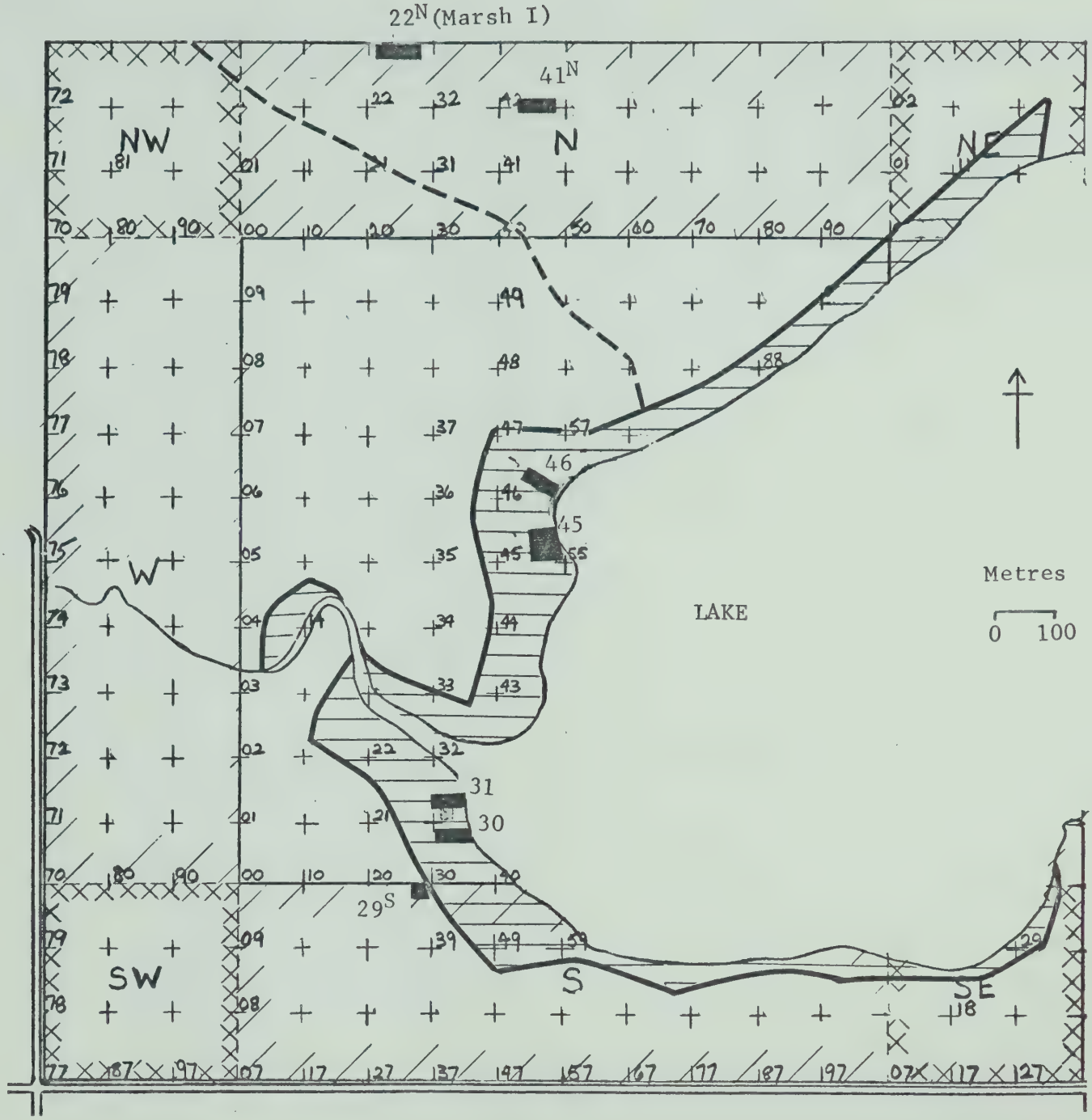
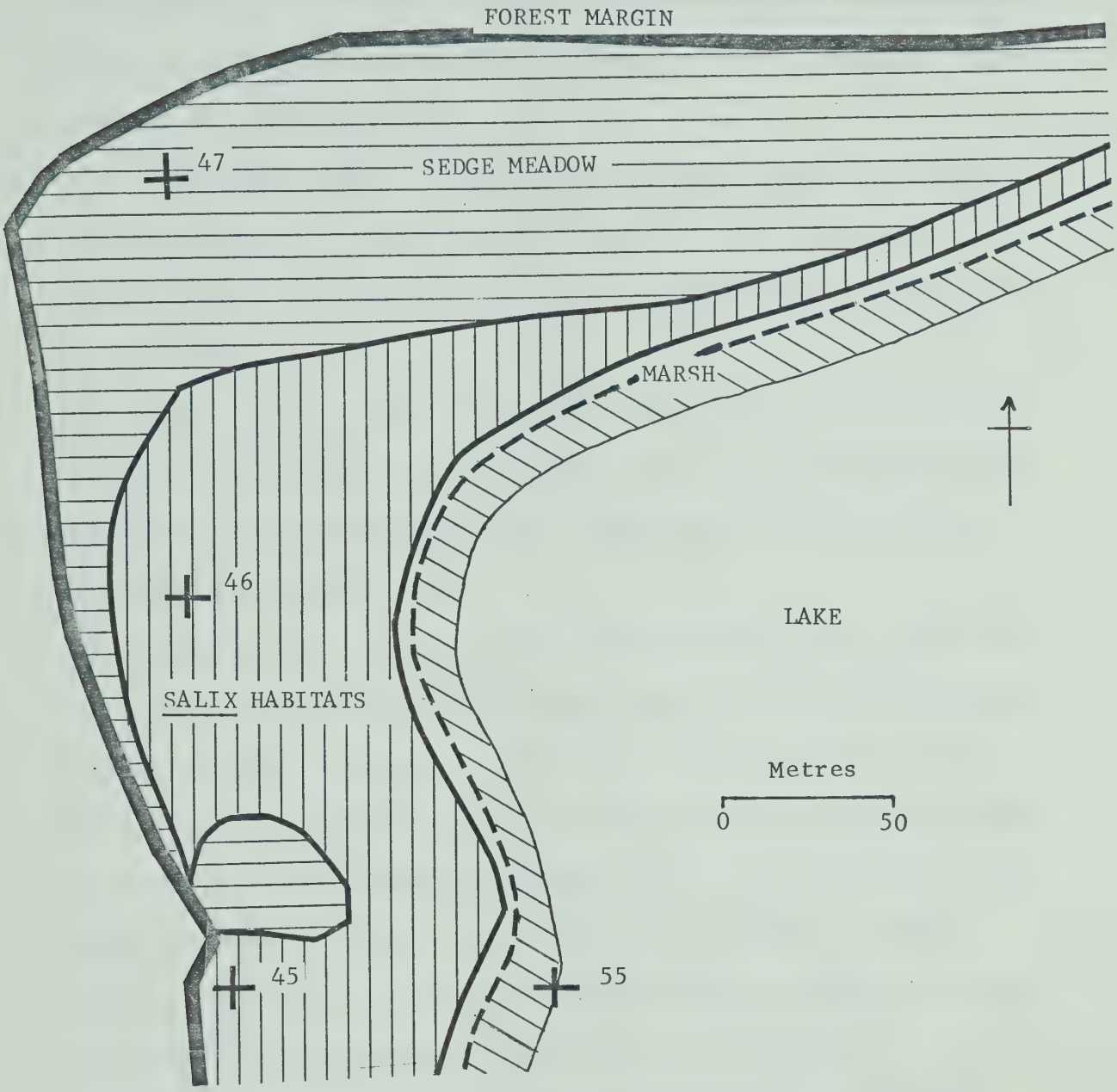

22N (Marsh I)
41N
NW
N
NE
W
LAKE
Metres
0 100
46
45
31
30
29S
SW
S
SE

Fig.2. Wet study areas, including 45 and 46, adjoining parts of the main marshes.

— — — indicates the frontier between shallow marsh and deep marsh habitats.

\+ indicates grid references


FOREST MARGIN
47
SEDGE MEADOW
MARSH
46
LAKE
SALIX HABITATS
Metres
0
50
45
55

Carex species among pools; leading dominants included *Carex aquatilis* Wahlenb., and *C. rostrata* Stokes. Patches of marsh marigold, *Caltha palustris* L., occurred also.

Transition zone. - Transition zones were delimited readily by (1) shallow marsh on one frontier bordered by *Salix* habitats; (2) forest margins on the other frontier. The main habitat types were the following.

(a) *Salix* habitats. These ringed the main marshes adjoining the lakeside. Specimens of *Carex rostrata* decreased in abundance where the willow growths were more dense. Moss and *Carex* associations occurred in low lying parts.

(b) Sedge meadows. These extended from *Salix* habitats, described above, but were isolated in other areas away from the main marshes. Hollows and pools abounded in these meadows and growths of *Carex rostrata* or *C. atherodes* Spreng. were dominant. Dead sedge formed litter which ranged from approximately five cm to 15 cm deep. This litter occurred in other wet habitats but was deepest in sedge meadows. Sometimes, sedge meadow habitats were divided up according to whether the vegetation was short *Carex* or tall *Carex*.

(c) Forest margins normally indicated the limit of waterlogged soil. Clumps of willows extended into the margins from sedge meadows. In more shaded forest margins very dense growths of nettle occurred among trees of *Aspen tremuifolia* Nutt. and *Populus balsamifera* L. Forest proper was defined by absence of sedges and sedge litter and the presence of leaf litter and humus, about three

to five cm deep and four to 10 cm deep respectively.

2.2.1. Physical differences between years

Changes in water levels and the limit of waterlogged soil were noted within and between years.

The melt waters from the 1967-1968 winter snows had largely gone by mid-June of 1968. Many hollows, waterlogged in spring, dried out by that date also. On May 20 a fire started along the northern boundary and swept across one sixth of the field station. Only one study area used in 1968 (Marsh I) was affected. There were periodic rains during June, July and August, but not more than one inch fell on any two successive days. Pools which formed quickly dried up, and there was no standing water in transition habitats in August or September.

Melt waters from the 1968-69 winter snows persisted throughout the summer of 1969. The levels of marsh water in May were higher than at any time in 1968. These water levels receded somewhat and some pools in sedge meadow dried out by late June. However more than one inch of rain fell on four separate days in July and August, and the water levels in the marshes rose again; many parts became flooded. Transition habitats largely became waterlogged and the amount of water in pools increased as the summer progressed. Further heavy rains in early September caused further flooding.

2.2.2. Study areas

Study areas were selected which included marsh and/or transition habitats (Fig. 1). Pitfalls were inserted along line transects in marshes, while line transects and grid systems of pitfalls were inserted in the main transition habitat types. Quadrats were sampled along line transects in the main habitat types. Details of sampling methods are included under field sampling.

The following study areas were sampled:

(A) Marsh I (station 22^{N}; Figs. 1 and 3, Table 1). This marsh was isolated from the main marshes and was along the northern boundary of the field station. The study area was surrounded by forest on all sides.

1968. - The fire on May 20 ringed the study area and cut across part of the trap systems. The main emergence sites of tenerals of *P. stygicus* and *P. lecontei* were surrounded by standing water and were not burnt over. The standing water had gone by the end of June and the marsh dried as the summer progressed.

1969. - The marsh was largely flooded throughout the 1969 season. Many flooded parts had little litter. The water level receded by mid-summer and rose again after heavy rains in early August (> four inches) and early September (> three inches). After the latter rains only parts of some logs were above water.

(B) Stations 45, 46, 30, 31, 29^{S}, and 22 (Figs. 1 and 2, Table 1). The last four were on the south side of the creek. The study areas here were classified according to habitat types:

Fig.3. Marsh I (station 22^{N}) showing pupal emergence sites, trap systems, areas of waterlogged soil and standing water in 1968 and 1969.

waterlogged soil in June of 1968. Only these parts of the study area were not burnt over by the May fire.

encloses area of standing water, May 1969.

encloses area of standing water, September 1969.

traps 1968, grid systems A and B.

traps 1969, line transects.

pupal emergence sites, 1968 and 1969.

Metres
0
5
Grid system B
Grid system A
NORTH BOUNDARY OF FIELD STATION
FOREST MARGIN

Table 1. Numbers of traps, pitfalls and cryptozoan boards, used at different stations between the end of May and the end of October (1968 - 1969).

Station(s)	(habitat)	Plastic 10cm diameter 1968 - 1969		Eavestroughing 175 x 10cm 1969	Boards of 250cm^2 alternating with those of 100cm^2 1969
41^N	(S.Me.,F.Ma.)	-	10(10)[1]	15	80
22^N; Marsh I	(M.,F.Ma.)	50	30	6	-
45,46	(M.,S.,S.Me.,F.Ma.)	50	56(56)	11	88
30,31	(M.,S.)	46	31(9)	16	-
29^S*	(F.,Ma.)	10	10(10)	-	-
22*	(S.,Me.)	10	10(10)	-	-
22^I	(S.)	20	10	-	-
	Total	186	157(95)	48	168

*of general trap system. [1]traps operating in October 1969.

M.,S.,S.Me., and F.Ma. indicate that traps were used in marsh, *Salix* habitats, sedge meadows, and forest margin respectively.

(1) Marsh - 45^{M*}, 46^{M}, 30^{M}, and 31^{M}. That at 31^{M} was less wet and more tussocky than the others, in 1968. It was not flooded in August of 1969 when study areas in other marshes were.

(2) Transition zone - (a) *Salix* habitats - 45^{I}, 46^{I}, 30^{I}, 31^{I}, and 22^{I**}. These habitats had little or no standing water in 1968 and were largely waterlogged by August of 1969. (b) Sedge meadows - 45^{I}, 46^{I}, 30^{I}, and 31^{I}. Most of the shallow pools in these parts dried out by early June 1968; they were then referred to as hollows. The amount of water in pools in 1969 increased as the season progressed.

(3) Forest margin - 29^{S}, 22 and $45^{F/P***}$. The last was a trap system in a hollow just inside the forest margin.

(c) Station 41^{N} (Fig. 1, Table 1). - This was a sedge meadow between Marsh I and a larger sedge meadow along the northern boundary of the field station. It was ringed by spruce forest on all sides. Much of this study area was transition zone which extended into spruce forest margin. This study area was burnt over by the May fire of 1968 but was not sampled during that year. Like other study areas in transition zones large parts of it became waterlogged, and hollows filled with water by August, 1969.

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*M stands for marsh habitats.

**I stands for intermediate (transition) zone habitats.

***F/P stands for forest pools.

3. Methods

3.1. Field sampling

Information on the sampling program is presented in Table 1. The sampling program differed in the two years because of periodic flooding of habitats and traps in 1969. Larvae and adults of the *Patrobus* species were rare in comparison with some other marsh carabids and much of the sampling had to be by pitfall trapping. Hand collections and quadrat counts, particularly in 1969, supplemented trapping. Cryptozoan boards (Cole, 1946) were used in the late summer and fall of 1969 to study the dispersal of larvae and adults from wetter habitats to drier overwintering quarters.

3.1.1. Trapping

Pitfall traps (lip diameter 10 cm) were used from May to November of 1968. In the spring of 1969, three quarters of these (Table 1) were flooded by the melt waters of the winter snows. I inserted 48 eavestrough lengths (hereafter called E-traps) of 175x10 cm and 169 small pitfalls in May and June of 1969 (Table 1). Heavy rains flooded these traps periodically during the summer and all were abandoned in early August. As the only pitfalls operating then were those in or near the forest margin, I inserted sufficient boards (see below) in two study areas to sample the carabid populations. At the end of September, I inserted another 48 small pitfalls in line transects extending from the marsh into the *Salix*

habitats at $45^{M,I}$ and 10 from the spruce stand into the marshy clearing at 41^{N}. Small traps in each of the line transects and grid systems were 2-2.5 metres apart.

During both summers traps were inspected every three to four days. Collections were made every week or two weeks in the fall and early winter of both years.

Where possible I have related pitfall catches to collections by other sampling methods. If not, I have restricted the analyses of trapping figures to providing presence and absence data, and to determining whether individuals were rare or abundant in the same or different habitat types. For example, adults of *P. lecontei* were sampled mainly by pitfalls, and only the range of seasonal and reproductive activity and the general distribution of adults in different habitats are outlined.

Various workers have pinpointed problems associated with pitfall trapping of carabids and Southwood (1966:195ff.) summarized these problems. In particular, Greenslade (1964) cautioned that pitfalls are best used with gonad dissections and with other methods of sampling such as hand collections, and then can be "used in comparing fauna of different habitats and for investigating the distribution of one species in a single vegetation type," and "for the qualitative assessment of different carabid faunas, especially when many species are restricted to one habitat or another." Other workers have indicated further problems associated with pitfall trapping of arthropods other than carabids. Joosse (1965),

Joosse and Kapteijn (1968) found that catches of surface dwelling Collembola were affected by roofs or covers over traps, the digging-in effect caused by insertation of traps, and disturbance of trap surroundings by collecting from traps. Hayes (1969) found that females of sand beach isopods and particularly gravid ones were less trappable than males, and suggested that similar biases might be found in trapping studies of other organisms.

Cryptozoan boards. - In August 1969 I placed cryptozoan boards (Cole, 1946) systematically in two stations. Large boards, of spruce of varying lengths but all 250cm^2 in area, alternated with small plywood ones (10x10cm). Each board was separated from its neighbour by a distance of 75cm. An area of vegetation and top soil corresponding to each board was cut out and the board pressed down in place. The boards were inserted in the following stations.

Station 41^N	Area I	two rows of twenty boards each, in the sedge meadow.
	Area II	two rows of twenty boards each, with half extending into a spruce stand and half extending into the sedge meadow.
Station 46	Area III	two rows of twenty boards in *Salix* habitats parallel to the marsh shoreline. The nearest row to the marsh was a distance of five metres from the water.
	Area IV	boards were placed in *Salix* habitats

along the periphery of a rectangle parallel to the marsh shoreline. There were four sides of twelve boards each. The nearest side to the marsh was 10 metres from the water.

I looked under the boards on August 24, September 12, September 26, October 12, and October 20. After the last date many boards were frozen to the soil's surface. Only larvae and adults of *Patrobus* species were collected from under these boards.

Daily activity studies. - The main periods of daily activity of adults of several populations of the four *Patrobus* species were studied. To do this I collected from pitfalls every three hours during 24-30 hour periods on August 17 and 18, 1968, June 27 and 28, and July 9 and 10, 1969. In 1968 collections were made from Marsh I. In 1969 collections were made from the tank experiment described below, and from the following study areas: (1) station 41^{N}, 10 E-traps in sedge meadow habitats, (2) Marsh I, five E-traps in shallow marsh, (3) 46^{P}, 58 small pitfalls in three pools with little standing water in sedge meadow.

A metal tank 82 x 28 x 15cm. was half filled with sieved soil and five females and males of the following were introduced:

Spring adults of *P. stygicus*

Summer tenerals of *P. stygicus*

Summer tenerals of *P. lecontei*

Spring adults of *P. foveocollis* and

early summer adults of *P. septentrionis*.

More specimens may have produced crowding effects. The tank experiment was adapted from Penney (1965) who measured the general activity of carabids kept in large plastic containers in the laboratory. Small glass tubes inserted in soil in the tank were used as pitfalls.

Collections were made less frequently during subsequent studies from mid-July to early August. I collected three times per day at 0600, 1500, and 2100 hours for periods of two to three days. These collections were made from 30 pitfalls in deep marsh, 30 pitfalls and five E-traps in shallow marsh, and 10 pitfalls and six E-traps in *Salix* habitats.

Window traps. - Four window traps (Chapman and Kinghorn, 1955) were inserted by mid-May 1969, and one more on August 21. I used 75x75cm sheets of glass. The traps were put in the following stations:

Marsh (shallow)	2 - $45,46^{M}$;	1 - Marsh I
Forest margin	1 - 45	
Sedge meadow	1 - 41^{N}	

Collections were made every two days from these traps until the end of August.

3.1.2. Hand collecting

I collected larvae, pupae and adults of the four *Patrobus* species by hand from May to November of both years. Three methods

were used. (1) Treading, I applied sufficient pressure with my feet to submerge the marsh vegetation; carabids were collected as they came to the water's surface. (2) Litter was sorted in the field and the field laboratory. (3) Pieces of peat and bark were carefully pulled from hummocks and logs with fine forceps to extract late third instar larvae, pupae, and their larval skins for rearing. A number of logs were brought to the field laboratory for examination by this method.

Most of these collections were biased but I also systematically hand collected per unit time in 1969. In the latter method, samples were taken from quadrats, of approximately 0.20cm^2, every three paces along line transects, during a period of 1.5 - 2 hours. This was useful in June and July, but not in August or later when the population densities of the *Patrobus* species were very low.

3.1.3. Quadrats

A one metre^2 frame subdivided by two partitions into four squares 0.5 metres on a side was used, alone in 1968, and with a hexagonal frame of 0.25 metre side and 0.20m^2 in area in 1969. In August and September 1969, samples were taken from quadrats of 0.05cm^2 in area in Marsh I. These samples were of necessity small because the sampling area consisted largely of fallen trees in deep marsh.

Random numbers were used to fix the position of random quadrats along line transects. On other occasions systematic

samples were taken at fixed distances along line transects, generally three metres, in deep marsh and in situations where large parts of the particular study areas were flooded. A number of contiguous quadrats were taken in 1969 to measure the dispersion of marsh carabids.

3.1.4. Mark and recapture

Individuals were marked by notching the apical portion of the elytron or elytra in various positions (Grüm, 1959). Mark and recapture was discontinued in 1969 as there was considerable emigration from study areas, when the beetles dispersed from flooded habitats.

3.2. Extraction of samples

Samples from random quadrats and hand collections made in 1969 were extracted by Tullgren funnels. Eight 14 inch and 12 10 inch diameter aluminum funnels with 25 watt bulbs were used.

3.3. Age grouping of carabids

Larvae which overwintered pupated in June and early July gave rise to summer adults. Adults which had overwintered to a second year were known as spring adults. Of the four *Patrobus* species at George Lake only *P. lecontei* overwinter solely as larvae.

Two types of criteria, sclerotization and colour changes in

the cuticle and the state of male and female gonads, were used for age grouping.

Sclerotization and colour changes. - The following three age classes of adults of *P. stycigus* were recognized in the field. (1) Teneral adults were characterized by pale coloured soft elytra. (2) Adults with soft elytra had tanned but not hardened cuticle. None of the six males and 20 females with soft elytra or eight males and 16 females with soft elytra dissected in 1968 and 1969 respectively were sexually mature. This indicated that adults of *P. stygicus* with soft elytra were all sexually immature. (3) Adults with hard elytra were sexually mature and sexually immature. Pressure was applied to elytra by the points of forceps in testing for hardness. Adults were classified as having soft elytra if small depressions were caused.

Adults of *P. lecontei* were classified into two age groups, namely tenerals and others. Individuals of this species became sexually mature shortly after completion of cuticular darkening, and a number of females with soft elytra carried eggs. Thus, the character of soft elytra was not useful for age grouping adults.

Only the same two age groups of *P. foveocollis* and *P. septentrionis* were recognized.

State of gonads. - Mature males were characterized by large accessory glands; mature females had eggs with egg shells (Gilbert, 1956). The number of mature eggs in field-captured females is an estimate of reproductive rate. This assumes that the rate at

which a female lays eggs is directly proportional to the number of mature eggs it contains. This was tested by Briggs (1957) who found it to be so with carabids of arable lands. Workers with carabids of other habitats (for example, H. Goulet, personal communication) have obtained similar results. Also, the following support the above assumption: (i) eggs at all stages of development can be seen in breeding females, (ii) the sharp increase in the number of mature eggs at the start of the breeding season and the relatively constant or gradually increasing numbers throughout the season.

4. *Patrobus stygicus* Chaudoir

General introduction. - Individuals of this species are the most hygrophilous of North American *Patrobus* (Lindroth, 1961). They overwinter both as adults and as larvae, and the species is transamerican extending into the conterminous United States only near Lake Superior (Lindroth, 1961).

4.1. Biology of larvae

Introduction. - Early instar larvae were usually difficult to sample and much of this section is based on observations of third instar larvae.

4.1.1. Distribution and activity of larvae, 1968

I hand collected extensively from mid-May to the end of June in 1968 and located late third instar larvae in the following habitats: (1) moss covered peaty soil hummocks by the lake shore in *Salix* habitats of the transition zone; (2) banks of moist to wet hollows; (3) decayed bark in the forest margins. Larvae were usually aggregated and the extent of aggregation was greatest in hummocks in *Salix* habitats. On May 24, 1968, I hand collected from one such hummock and extracted 25 larvae from an area of approximately one square metre and seven centimetres deep. Only occasional larvae were sampled between these hummocks. Some pupated by May 24, but most pupated by the end of June.

I first trapped larvae, between September 15 and September 29, within the marsh and *Salix* habitats at station 31. Between September 29 and October 5, larvae were first trapped in the shallow parts of the other marshes. The number of larvae/10 traps per day in the marshes at peak activity between October 6 and October 12 was between 1.4 and 1.6. Few larvae were trapped in the deep marsh at 45^{M}, i.e., in traps between 12 and 22 metres from the willows, though adults were active throughout the marshes in August (Table 7). Activity decreased by half between October 14 and October 26. By the last date larval activity increased in *Salix* habitats and hollows in the transition zone. This was exemplified by a large increase in activity in a large hollow, 46^{P}.

Very few larvae of *P. stygicus* were trapped in the isolated Marsh I in comparison with the main marshes. Peak activity was between October 5 and October 12.

4.1.2. Distribution and activity of larvae, 1969

Larvae were hand sampled at 31^{I}, from similar habitats as those in 1968, but none were collected from such habitats at other stations.

On August 5 early second instar larvae were sampled from tussocks in shallow marsh at 45^{M}. The sampling area at Marsh I in August consisted of decaying bark and some tussocks in water, approximately one metre deep. Further heavy rain at the beginning of September caused the water to cover the remainder of the

tussocks; larvae were then confined to the very wet logs. Larvae were clumped in both August and September (Table 2).

Larvae were trapped first between September 27 and October 5 and peak activity was between October 13 and October 18, one week later than in 1968. The number of larvae trapped in *Salix* habitats between October 13 and October 18 were: within 10 metres of the marsh, 20 larvae/20 traps or 1.52/10 traps per day; within 10 and 22.5 metres of the marsh, 3 larvae/20 traps or 0.25/10 traps per day. By November 9 they were active throughout the lengths of pitfall transects (Table 3). Between then and November 24, activity within 2.5 metres of the frozen marsh was nil. Activity practically ceased by the latter date for only two larvae were trapped between then and December 9.

4.1.3. Discussion

Early second instar larvae were aggregated in tussocks and low lying bark in marshes in August 1969. This and the fact that larvae were most active in shallow marsh in 1968 indicated that their main emergence sites, and therefore the main oviposition sites of females, were probably in marsh *Carex* tussocks.

Flooding of habitats probably affected the distribution of larvae in the late summer and fall of 1969. Larvae were confined to very wet logs in Marsh I when the water covered tussocks. There were no fallen trees or dead logs in the main marshes, and tussocks were the only suitable habitats for larvae before the

Table 2. Numbers of larvae of *Patrobus stygicus* collected in quadrats from different habitats in 1969.

	Main marsh (45^M)	Marsh I (22^N)		*Salix* habitats (45^I)	Spruce to sedge meadow (41^N)
	Aug.5	Aug.23	Sept.12	Oct.18	Oct.19
Numbers of Larvae	4(II)	8(II)	6(III)	1(III)	-
Numbers of Quadrats	6	12	12	22	10
Size of Quadrats in m^2	0.20	0.05	0.05	0.20	0.20
Mean density $/m^2$	3.34	13.34	10.0	0.23	-

Quadrats sampled in Marsh I were of necessity small because the sampling area consisted largely of fallen trees in deep marsh.

Roman numerals in parentheses indicate the instar of larvae.

Table 3. Numbers of larvae of *Patrobus stygicus*/10 traps per day trapped, between October and December 1969, in *Salix* habitats bordering the main marshes.

Date of collection	Numbers of larvae/10 traps per day		
	Collected between 0m - 10m from marsh	Collected between 12.5m - 22.5m from marsh	Collected between 0m - 22.5m from marsh
12.x	0.12 (2)[1]	0.19 (3)	0.33 (5)
18.x	1.52 (20)	0.25 (3)	0.92 (23)
26.x	0.34 (6)	0.06 (1)	0.17 (7)
9.xi	0.75 (23)	0.50 (14)	0.58 (37)
24.xi	0.15 (5)	0.13 (4)	0.14 (9)
8.xii	- (0)	0.04 (1)	0.02 (1)

Traps were 2.5 metres apart in each of four transects, and there were 10 traps in each. [1]Figures in parentheses indicate the numbers of larvae taken from each set of traps at each collection.

water covered the tussocks. I sampled early second instar larvae of *P. stygicus* from such tussocks in August 1969. The rain in early September caused the marsh water to cover many of the tussocks and so rendered them uninhabitable for larvae. However, as larvae occurred in Marsh I in very wet situations, flooding may not have caused high larval mortality in the main marshes and they may have dispersed into *Salix* habitats. By October most larvae appeared restricted to *Salix* habitats and a narrow strip of shallow marsh.

Aggregations decreased as larvae became more active. Peak activity in both years was between early and mid-October. The high activity of larvae in less wet parts of *Salix* habitats in late October was probably related to dispersal to drier overwintering sites. Late third instar larvae were aggregated in hummocks and bark *et cetera* (4.1.1.) in transition habitats in May and June. Larvae would not have dispersed far from their overwintering sites by May. Thus they either overwintered in these hummocks and bark or in the vicinity of them, possibly in the soil beneath.

The composition of populations of larvae with respect to proportion of progeny of spring and summer adults differed between years. In 1968, most if not all of the larvae trapped were progeny of summer adults. Spring adults were rare that year (4.2.1.1.) and consequently probably left few progeny. In 1969, the populations of larvae probably contained progeny of both spring and summer adults, as the periods of reproductive activity of both spring and summer forms overlapped (4.2.2.2.). The second instar larvae

sampled in the marshes in early August were progeny of the spring adults as spring females carried mature eggs from late May on, and summer adults probably did not breed until late July. Third instar larvae trapped from late September of 1969 on, likely included larvae of both spring and summer adults, as third instar larvae of summer adults were collected from mid-September on, in 1968.

In summary it appears that the range of distribution of larvae was affected by habitat flooding and by dispersal, from marshes and wet parts of *Salix* habitats *et cetera*, to drier overwintering quarters. The range was greatest during the period of main activity, that is October, and least prior to and just after overwintering. Larvae predominated in shallow marsh and *Salix* habitats during their period of main activity. By early winter they occurred mainly in drier parts of *Salix* habitats and were aggregated in hummocks, bark *et cetera* in these habitats the following spring.

4.2 Biology of adults

4.2.1. Distribution and activity, 1968

Introduction. - Unlike many carabid populations of drier habitats, a number of marsh carabids at George Lake had very distinct and localized pupal emergence sites (described above, 4.1.1.). I studied the habitat distribution of adults of *P. stygicus* during the season in relation to these sites. Traps were inserted

close to emergence sites at Marsh I, trap system A; at $45^{F/P}$, near the forest margin; and at 31^{I}, in *Salix* habitats. Other trap systems in the study areas were inserted away from the vicinity of these emergence sites, for example trap system B in Marsh I (Fig. 3).

I followed Grüms example (1962) of comparing the sex ratio of adults in different age groups trapped in the different parts of each study area, so as to delimit the living quarters of males and females, throughout the season. The sex ratio is the number of females over the number of males and females; it ranges from 0 to 1.

4.2.1.1. Summer adults

Few spring adults were trapped or hand sampled in May and early June; none were trapped later.

I hand sampled summer tenerals from pupal cells in peaty hummocks and other emergence sites between mid-June and June 30. Tenerals were first trapped between June 24 and June 26. The numbers of males and females trapped at the different stations/ habitats are summarized in Table 4. Before mid-July, it is evident that more females were trapped in stations near to emergence sites - $45^{F/P}$, 31^{I} and Marsh I - A, while the sex ratio of catches in other habitats was about 0.5. In August the sex ratio of carabids trapped in the main marshes was 0.5, whereas it varied in Marsh I in different areas.

The collections at Marsh I in August were characterized by a

Table 4. Numbers of adults of *Patrobus stygicus* in each of three age groups, and their sex ratio, trapped in different habitats in July 1968.

Habitat (Station)	Age Group	Tenerals	Adults with soft elytra	Adults with hard elytra	Total
Hollow near forest margin ($45^{F/P}$)	1 - 16.vii.	- 1F (1.0)	2M 8F (0.80)	6M 16F (0.74)	8M 25F (0.78)
	17 - 28.vii.	- -	5M 5F (0.50)	4M 5F (0.56)	9M 10F (0.52)
Marsh I (22^{N} - A)	2 - 14.vii.	- -	- -	- -	8M 21F (0.73)
	15 - 31.vii.	1M - (0.0)	5M 17F (0.78)	4M 17F (0.80)	10M 34F (0.77)
(22^{N} - B)	2 - 14.vii.	- -	4M 4F (0.50)	12M 10F (0.46)	16M 14F (0.47)
	15 - 31.vii.	1M - (0.0)	13M 20F (0.61)	31M 25F (0.43)	45M 45F (0.50)
Salix habitats (31)	2 - 12.vii.	- 1F (1.0)	1M 2F (0.67)	13M 17F (0.58)	13M 20F (0.60)
	13 - 30.vii.	3M 1F (0.25)	5M 8F (0.61)	9M 6F (0.37)	17M 15F (0.47)

The sex ratio, no. of females/nos. of males and females, is indicated in parentheses. M and F indicate males and females respectively.

high number of adults with soft elytra; 35 adults with soft elytra and 74 adults with hard elytra were trapped. It is interesting to compare the catches, between study areas in the main marshes, in relation to degree of wetness of habitat. In the drier marsh at 31^{M} the ratio of the number of adults with soft elytra to the number of adults with hard elytra was 3 : 6 while the ratio at 45^{M}, the wetter marsh, was 4 : 42. No female dissected prior to July carried mature eggs.

By August 1, adults were active throughout the main marshes from shallow marsh to the lakeside. Activity decreased sharply after August 3 and ceased after August 18; during this period few adults were trapped in the transition zone (Table 5).

Some samples were taken from random quadrats of one metre^2 in the marshes in July and August, and carabids were extracted by treading (3.1.). Six samples were taken on each occasion and each sampling period corresponded to about two hours of intensive hand collecting. I collected four males, one male, three males, and one female from random quadrats on July 18, July 26, August 10 and August 15 respectively. On August 15, six quadrats were sampled and one female was obtained.

Of the 33 adults trapped in September and October, eight were in *Salix* habitats of the transition zone, 19 were in or near the forest margin, and only one adult was in the marshes (Table 6).

Possible oviposition sites. - The habitat distribution of females trapped in August and of larvae trapped between October 5

Table 5. Numbers of adults of *Patrobus stygicus* in each of two age groups, and their sex ratio, trapped in August 1968.

Habitat (station)	Adults with soft elytra			Adults with hard elytra		
Hollow near forest margin ($45^{F/P}$)		2F	(1.0)	1M	1F	(0.5)
Salix habitats (45^{I})		2F	(1.0)	2M	1F	(0.34)
Marsh (45^{M})	1M	3F	(0.75)	21M	21F	(0.5)
Salix habitats (31^{I})		3F	(1.0)		2F	(1.0)
Marsh (31^{M})	2M	1F	(0.34)	4M	2F	(0.34)
Marsh I (22^{N})						
Trap system - A	6M	6F	(0.5)	7M	12F	(0.63)
Trap system - B	7M	16F	(0.69)	25M	23F	(0.48)

The sex ratio is indicated in parentheses. M and F indicate males and females respectively. Sex ratio is defined in Table 4.

and October 12, in the marsh at 45^{M} is given in Table 7. Though adults ranged from shallow marsh to the lakeside, most larvae were trapped in the first half of the line transects. Larvae were also active in *Salix* habitats in the same period (4.1.1.).

4.2.1.2. Discussion

The catches made in the last two weeks of July (included in Table 4) and the month of August (Table 5) were analyzed in two three way tests of independence. The stage of development was indicated by the hardness of elytra. As described above (3.3.) adults with soft elytra were sexually immature and older adults with hard elytra were either sexually immature or sexually mature. Adults were classified according to three factors: sex, whether they had hard elytra or soft elytra, and habitat. For ease of calculation I employed the G-test (Sokal and Rohlf, 1969), the distribution of which can be approximated by the χ^2 distribution.

There was no significant difference between the frequencies of the age groups according to sex or station/habitat in July, but the frequencies of males and females differed according to habitat (Table 8). The sex ratio of adults with soft elytra and those with hard elytra trapped near the emergence sites were high, about 0.8. That is, more females of both age groups were trapped near these sites. The distribution of females in July was not correlated with oviposition sites as dissections indicated that females had not mature eggs until early August. By this time

Table 6. Numbers of males and females of *Patrobus stygicus* trapped in different habitats during September and October, 1968.

Habitat	No. of traps	Numbers of adults
Main marshes	68	1F
Salix habitats	38	2M 6F
Forest margin	37	12M 7F
Marsh I	48	1M 4F

Table 7. Numbers of males and females of *Patrobus stygicus* trapped in August 1968, and the number of larvae trapped between October 5 and October 12, 1968 in the main marsh at 45^{M}.

No. of traps	Distance of traps into marsh in metres	Adults	Larvae
12	0 - 10	3M 5F	9
		5M 5F	19
12	12 - 22	5M 4F	2
		2M 1F	4

Pitfalls were two metres apart in two line transects which extended from shallow marsh to the lakeside. M and F indicate males and females respectively.

Table 8. Summary of three way G-test of independence analysis of adults of *Patrobus stygicus* trapped in the last two weeks of July 1968.

Hypothesis tested	*d.f.*	*G*
H x S independence	3	11.464 ** P < 0.01
$45^{F/P}$ vs. 31^{I}	1	0.017
Marsh I - A vs. - B	1	10.346 *** P < 0.005
$45^{F/P}$ + 31^{I} vs. Marsh I - A + - B	1	1.084
S x A independence	1	2.45
H x A independence	3	3.268
H x S x A interaction	3	1.13
H x S x A independence	10	18.312 * P < 0.05

H, S, and A denote factors: habitat, sex and age group respectively. Asterisks indicate that the hypothesis is rejected, the level of significance is shown after the asterisks.

they had dispersed away from the area of the emergence sites.

Of the beetles collected in August, the main period of reproductive activity, there was a significant difference between the frequencies of age groups according to sex and stations/habitats (Table 9). This G (approximate χ^2) was partitioned by grouping habitats into two classes, namely those in Marsh I and those in other study areas. A significantly greater number of adults with soft elytra were trapped in the drier Marsh I than in the wetter areas of the main marshes. In these latter areas the overall ratio of adults with hard elytra to adults with soft elytra was high. Thus, most adults with hard elytra were collected in wet areas.

Larvae predominated in tussocky parts of marshes and were infrequently collected in *Typha* regions. I suggested above (4.1.3.) that tussocks appeared to be the only suitable sites for oviposition in marshes. As larvae were also active in *Salix* habitats in early October, that is prior to their period of peak activity, females may have oviposited in shaded parts of this region also.

4.2.2. Distribution and activity, 1969

Introduction. - Only parts of the periods of seasonal activity of spring and summer adults were studied in July and August because of periodic flooding of traps, and much of the data presented were obtained from stations 45 and 46.

Table 9. Summary of three way G-test of independence analysis of adults of *Patrobus stygicus* trapped in August 1968.

Hypothesis tested	*d.f.*	*G*	
H x A independence	3	16.30 **	P < 0.01
Main Marsh vs. Marsh I	1	4.011 *	P < 0.05
H x S independence	5	7.444	
S x A independence	1	3.938 *	P < 0.05
H x S x A interaction	5	6.296	
H x S x A independence	16	33.978 **	P < 0.01

For explanation of symbols see footnote to Table 8.

The extent of aggregation of adults in various habitats in May and June was measured by sampling from contiguous quadrats on different occasions. This was related to dispersal of adults from the vicnity of overwintering sites to wetter habitats prior to the main egg laying period. To measure dispersion and 'mean crowding' (Lloyd, 1967) I took a series of 17 contiguous quadrats of 0.20 metre^2, on June 2 for example, in a small marshy clearing between Marsh I and 41^N. 'Mean crowding' can be measured by the mean number per individual of other individuals in the same quadrat. Statistically, 'mean crowding' is the amount by which the ratio of sample variance to mean density exceeds unity, added to the mean density itself so, $m^* = \bar{x} + \left(\frac{s^2}{\bar{x}} - 1 \right)$ (Lloyd, 1967).

4.2.2.1. Spring and summer adults

Extensive sampling was done in May and June of 1969 (Table 10). Spring adults were found in aggregation under bark in shallow marsh in Marsh I, in shallow pools in sedge meadow at 41^N on May 10, and in hollows near forest margins. Aggregations decreased as the season progressed. On May 11, the mean density, $\bar{x}$, was 0.38 per quadrat or 1.5/m^2 and m*, the index of crowding, was 0.05 other individuals per quadrat per individual; this distribution approximated to randomness. On May 29, adults were highly aggregated, $\bar{x}$ was 3.63/quadrat or 14.5/m^2 and m* was 5.14. Five males and two females were extracted from 17 quadrats, on June 2 in a marshy clearing; $\bar{x}$ was 0.41 adults per quadrat or 2.1/m^2; m* was 0.65.

Table 10. Numbers of males and females of spring adults of *Patrobus stygicus* hand and quadrat collected in 1969

Habitat	Marsh I	Hollow	Main Marsh	Marsh I	Hollow	Marshy clearing	Marsh (outside George Lake)
	May 10	May 11	May 18	May 26	May 29	June 2	June 8
No. and sex of specimens	1M 7F	6F	2M	7M 15F	12M 17F	5M 2F	3M 4F
Number of quadrats	-	16	-	8	8	17	-
Methods of collection	(H.coll)	Q	(H.coll)	Q	Q	Q	(H.coll)
Size of quadrat	-	$0.25m^2$	-	$1m^2$	$0.25m^2$	$0.20m^2$	-

(H.coll), Q, M, and F indicate hand collections, quadrats, males and females respectively.

Apart from the May 10 collection, samples with a high percentage of females were taken from hollows (Table 10). On May 26, three males, 11 females were collected from contiguous quadrats in shallow marsh, but an equal number of males and females were sampled from random quadrats throughout the marsh. The total number of carabids collected on May 26 is indicated in Table 10.

The main emergence period of summer tenerals was from June 20 to June 28. Their sudden appearance was illustrated by catches made in *Salix* habitats at 31^{I} between June 24 and June 28 (Table 11). By the latter date, tenerals were active in pools and shallow marsh also. The number of spring adults and summer tenerals trapped during a 24 hour period on June 27 and June 28 were: in sedge meadow at 41^{N}, 21 spring adults and three summer tenerals; in pools in sedge meadow, 25 spring adults and four summer tenerals; in shallow marsh at Marsh I, two spring adults and three summer tenerals. The elytra of most summer adults hardened by early July, and spring and summer adults could not be distinguished from one another.

Water levels decreased somewhat in July. After late July the number of adults trapped in *Salix* habitats and shallow marsh decreased and the number of adults trapped in the deep marsh increased. Twenty-five, 21, and 21 adults were trapped in *Salix* habitats, shallow marsh, and deep marsh respectively, between July 18 and July 25. Twelve, four, and 48 adults were trapped in *Salix* habitats, shallow marsh, and deep marsh respectively, between July 26 and August 3.

There was a marked decrease in numbers of adults collected in all habitats after mid-August. Hand collections (Table 12) and trapping showed this clearly, and only one adult was collected from under boards in September. Also, no adults were sampled from 22

Table 11. Numbers of spring and summer adults of *Patrobus stygicus* trapped at 31^{I} in *Salix* habitats in late June of 1969.

	Spring adults		Summer tenerals	
24.vi.	3M	1F	1M	1F
25.vi.	3M	1F	4M	2F
28.vi.	2M	2F	5M	4F

Table 12. Numbers of adults of *Patrobus stygicus* hand collected per two hours in marshes at different stations in 1969.

Marsh I	45^{M}	46^{M}, 47^{M}	45^{M}
July 12	Aug.17	Aug.19	Aug.21
6	9	0	2

random 0.20m^2 quadrats in transects from the marsh - transition frontier into *Salix* habitats at 45^I on October 18; nor from 10 samples also from 0.20m^2 quadrats along a transect from spruce forest margin into sedge meadow at 41^N on October 19. Neither were any adults hand collected or trapped in October.

Reproductive activity. - Gravid spring females were collected first in late May. One male, three females of the spring adults sampled from quadrats on May 26 at Marsh I were dissected. One female carried mature eggs. A spring adult which was marked and released in Marsh I on August 17, 1968, was recaptured in the same study area on July 17, 1969. It carried mature eggs. Egg laying began in late May and continued through June, July and August (Table 13).

Daily activity rhythms. - Spring and summer adults were trapped during daily activity studies. Except for soft bodied summer tenerals, no attempt was made to define activity rhythms for the two forms. Adults were active during day and night. Tenerals were nocturnal mostly and were restricted to *Salix* habitats and shallow marsh. The activity rhythm of one teneral trapped in the tank experiment was nocturnal.

4.2.2.2. Discussion

Sampling began in early May, but most spring adults had emerged already from their overwintering quarters. These quarters included bark in forest margin and *Salix* habitats. In May, adults of *P. stygicus* were aggregated in the vicinity of overwintering

Table 13. Gonad dissections of females and males of *Patrobus stygicus*.

		1968				1969			
		June	July	Aug.	Sept.	May	June	July	Aug.
	x	n	n	n	n	n	n	n	n
	0	5	12	26	9	4	7	4	8
	1 - 20			8		2	11	16	10
FEMALES	21 - 40							5	
	Σ N	5	12	34	9	6	18	25	18
			n	n		n	n	n	n
MALES	Immature		0	6		1	5	3	1
	Mature		5	6			2	21	5
	Σ N		5	12		1	7	24	6

n = number of females or males examined

x = number of mature eggs per female

Females are grouped into three classes according to the number of mature eggs each contained.

Males were classified as immature or mature.

sites, for example hollows near forest margin. Aggregations decreased as carabids dispersed to wetter habitats in sedge meadows and shallow marsh. Many males may have dispersed before sampling began as shown by the predominance of females in hollows in May, and by the different distribution of males and females in Marsh I on May 26. On the latter occasion, females predominated in shallow marsh and males were more common in deeper parts.

Summer tenerals emerged in late June. This emergence period afforded me the only opportunity of delimiting the spring and summer adults, as the latter were characterized by very soft elytra. Daily activity and 24 hour studies indicated that adults of both forms occurred together in pools in sedge meadows, *Salix* habitats, and shallow marsh.

Females carried mature eggs in late May, June, July, and August of 1969. Those collected in May and June were spring females, because summer adults were not active until late June. Most gravid females sampled in July of 1969 were probably spring adults too, as: (1) no gravid summer females were collected before late July in 1968; (2) a spring female marked in 1968 and recaptured in mid-July, 1969 carried mature eggs.

The marsh water levels decreased in mid-July and summer adults and possibly spring adults dispersed out into deep marsh. Adults were active mainly in the marshes in early August. Pitfall trapping, collections from boards, hand collecting, and quadrat counts indicated a marked decrease in numbers of adults in all

habitats after mid-August. This was in contrast with the late summer and fall of 1968 when carbids were relatively active in transition habitats. The 1969 data show that any one of the above sampling methods could be used to determine if populations were rare or abundant.

A large number of adults with soft elytra were collected in the dry summer of 1968 (Tables 4 and 5), but relatively few in the wet summer of 1969. A comparison of catches made in the last two weeks of July, after the main period of teneral emergence, in both years (Table 14) shows a highly significant difference between the numbers of adults with soft and hard elytra trapped ($G = 18.756$, $P < 0.001$). Thus a significantly greater number of older individuals were collected in 1969. The high activity of adults in the deep marsh and the very low activity in *Salix* habitats was very striking. This paralleled my observations of 1968, of the predominance of adults in the marshes during the egg laying period.

4.2.3. Summary of data of 1968 and 1969

Spring adults were aggregated in the vicinity of overwintering sites in May. They dispersed to wetter habitats, such as *Salix* ones, pools in sedge meadows, and shallow marsh for breeding. Summer tenerals emerged in late June and occurred in the same general habitats as spring adults. Summer adults, and possibly spring adults, dispersed into deep marsh as the water levels decreased. The periods of reproductive activity of both forms overlapped.

Table 14. Numbers of adults of *Patrobus stygicus* with soft and hard elytra trapped in marsh and transition habitats between July 14 and July 31 in 1968 and 1969.

Habitats	1968		1969	
	Soft elytra	Hard elytra	Soft elytra	Hard elytra
Transition	27	24	11	23
Marsh	57	77	6	86
	84	101	17	109

Females probably oviposited in shallow marsh and in wetter parts of transition habitats. Age composition of populations differed within and between years according to differences in levels of standing and soil water.

In fall, the range of distribution narrowed as the beetles dispersed to drier areas prior to overwintering.

5. *Patrobus lecontei* Chaudoir

Introduction. - This species is almost transamerican but is not represented on the Pacific coast. Adults occur mainly near standing water, many immatures are active in early summer and populations appear to overwinter in the larval stage only (Lindroth, 1961).

5.1. Distribution and activity of larvae, 1968 - 1969

Pupation sites. - The occasional late third instar larva was trapped in May of either year. Late third instar larvae and pupae were hand collected mainly from bark in litter in forest margin, and banks of hollows and pools, but in June of 1968 three pupae were hand collected from grey soil in the forest at station 34.

Fall to early winter activity, 1968. - One larva was trapped between September 14 and September 28. Peak activity was between October 5 and October 12. Most larvae were trapped in *Salix* habitats, in which 12 larvae/30 traps or 0.5/10 traps per day were collected, but some were trapped in shallow marshes. Few larvae were trapped in hollows in the transition zone before mid-October but their numbers there increased sharply by October 26.

The number of larvae trapped in Marsh I was very low in comparison with other study areas for 0.056 to 0.060 larvae/10 traps per day were collected in the former. These few larvae were trapped only in trap system B, farthest away from the emergence sites.

Fall to early winter activity, 1969. - No larvae were sampled until October 13. Between October 18 and November 9, 17 larvae per 40 traps were trapped in *Salix* habitats bordering the main marshes. No larvae were trapped after November 9.

5.2. Distribution and activity of adults, 1968 - 1969

5.2.1. Seasonal activity, 1968

Tenerals were hand collected from pupal cells, in habitats described above (5.1.) from mid-June to end of June. Larvae pupated early in June and probably late in May.

Adults were trapped near the area of teneral emergence sites in Marsh I until mid-July. After this date they were trapped mainly in areas away from these sites (Tables 15 and 16). A comparison of catches made in the first two weeks of July and between mid-July and the end of August shows a highly significant difference between the numbers of adults trapped near the emergence sites and away from the emergence sites ($G = 24.358$, $p < 0.001$).

Reproductive activity. - Adults came into breeding condition shortly after emergence. One female dissected carried mature eggs in June 25. The entire egg production period was not defined but it likely coincided with the main activity period, between July 3 and August 3 (Table 17). Mature eggs were found in females during July and August. Most specimens trapped in August were encrusted with heavy mite infestations. No adults were sampled after August in any study area.

Table 15. Numbers of adults of *Patrobus lecontei* and their sex ratio, trapped in 1968

	2 - 14.vii	15 - 31.vii	1 - 15.viii	16 - 31.viii
Marsh I (Trap system A)[1]	10M 13F (0.57)	2M 5F (0.7)	-	-
Marsh I (Trap system B)[2]	8M 8F (0.5)	39M 26F (0.4)	9M IF (0.1)	1M (0.0)
Hollow near forest margin ($45^{F/P}$)	7M 4F (0.36)	16M 11F (0.41)	1F (1.0)	-
Salix habitats (31^{I})	6M 4F (0.4)	4M 4F (0.5)	1F (1.0)	1F (1.0)

The sex ratio, no. of females/nos. of males and females, is indicated in parentheses. M and F indicate males and females respectively. [1]Traps near teneral emergence sites. [2]Traps away from teneral emergence sites.

Table 16. Numbers of adults of *Patrobus lecontei* trapped near and away from teneral emergence sites in Marsh I in 1968

	Adults trapped near emergence sites	Adults trapped away from emergence sites
2.vii - 14.vii	23	16
15.vii - 31.viii	7	76
	30	92

Table 17. Gonad dissections of females and males of *Patrobus lecontei*

		1968		1969		
		July	Aug.	June	July	Aug.
	x	n	n	n	n	n
	0	1	1		1	1
FEMALES	1 - 20	3	4	2	13	5
	21 - 40	1	1	1	9	3
	41 - 60	2			2	0
	ΣN	7	6	3	25	9
		n	n	n	n	n
MALES	Immature	0	2	0	3	0
	Mature	1	1	5	14	4
	ΣN	1	3	5	17	4

n = number of females or males examined

x = number of mature eggs per female

Females are grouped into four classes according to the number of mature eggs each contained. Males were classified as immature or mature.

5.2.2. Seasonal activity, 1969

Tenerals were hand collected from mid-June on and were trapped first on June 20, a few days earlier than in 1968. Most adults were trapped in *Salix* habitats, in marshy parts, e.g. 41^{N}, and pools in sedge meadows. Few were trapped in Marsh I and these were near the marsh periphery. In the shallow marsh of study areas adjoining the lakeside, I first trapped adults on July 9 and most adults were trapped after mid-July. Between July 18 and August 3, 36 adults and 80 adults were trapped in shallow marsh and *Salix* habitat respectively. Adults were active in the field during day and night throughout the season, although six adults were trapped in the tank experiment between 20.30 hours and 05.30 hours on June 27 and June 28.

Reproductive activity. - Females carried mature eggs from late June into August (Table 17). The last females with mature eggs were trapped between August 15 and August 17. As in 1968 no adults were sampled after late August.

Coition occurred in long E-traps from late June to early August, but rarely in small pitfalls. On three different occasions a second male attempted to mount a female when another male was already copulating.

5.3. Discussion

Though tenerals were trapped in *Salix* habitats, for example,

no pupae were sampled from hummocks like those in which *P. stygicus* pupae were found (4.1.1.). Larvae probably pupated in soil in *Salix* habitats. As noted, pupae were extracted from bark in litter in forest margin, and a few from soil in deep forest. The latter habitat may have been atypical but these observations support my suggestion that larvae normally pupated below soil level.

Adults were characterized by rapid development of sexual maturity, for females with soft elytra carried large immature eggs shortly after the main emergence period. Adults were active mainly in *Salix* habitats and in hollows and shallow pools in sedge meadows. In these habitats, females carried mature eggs from late June to late August. The heavy mite infestations of adults sampled in August probably indicated old age of these beetles. None were collected after this month and it can be assumed that most adults died by the end of August. Thus, they lived for approximately 2-1/2 months, from mid-June to the end of August.

In 1968 adults and larvae predominated in *Salix* habitats and hollows in sedge meadows, but individuals of both stages were trapped in shallow marsh. These facts indicate that the main oviposition sites were *Salix* habitats and sedge meadows, but that some females may have oviposited in parts of marshes. In Marsh I most adults and all early third instar larvae were trapped away from the emergence sites of tenerals (Trap System B). These facts suggest that females oviposited away from the vicinity of the emergence sites, in 1968. Though third instar larvae were active only in *Salix* habitats in the

fall of 1969, it is not possible to infer the occurrence of main oviposition sites of that year. If females also oviposited in shallow marsh their larvae could have drowned or dispersed into *Salix* habitats in August and early September.

In summary, populations of *P. lecontei* overwintered as larvae. Larvae pupated both below and above soil surface. Tenerals emerged in June but few were collected, because adults were characterized by a short period of development. Females carried eggs in late June shortly after the main teneral emergence period, and egg laying continued until late August. More adults were trapped in sedge meadows and *Salix* habitats than elsewhere. No adults were sampled after August, so the life span of the adults was probably not more than 2.5 months. Only third instar larvae were sampled and these mainly in transition habitats.

6. *Patrobus foveocollis* Eschscholtz

Introduction. - Populations of this species have no association with standing water and individuals are the least hygrophilous of North American *Patrobus* Lindroth, 1961). The geographical distribution of *P. foveocollis* is transamerican, and populations occur in easternmost Siberia also (Lindroth, 1961).

6.1. Distribution and activity of larvae, 1968 - 1969

Larvae were rare in the fall of 1968 and were trapped in Marsh I and forest margins. Four third instar larvae only were collected from 50 traps in Marsh I; three were trapped between September 29 and October 5.

In 1969, one second instar larvae was extracted from bark in a hollow near forest margin on August 12. Third instar larvae were collected from under boards from September 12, and were pitfall trapped first between October 8 and October 12. In *Salix* habitats, most larvae were trapped between October 13 and October 18. No specimens were collected after November 24 (Table 18). Larvae were very active in other study areas also. The number of larvae trapped between September 25 and October 18 were: in forest clearings (83^{W} and 84^{W}), 15 larvae/20 traps or 0.33 larvae/10 traps per day; in forest margins (29^{S},22), 20 larvae/20 traps or 0.43 larvae/10 traps per day; and in *Salix* habitats (45^{I}), 11 larvae/20 traps or

Table 18. Numbers of larvae of *Patrobus foveocollis*/10 traps per day trapped, between October and December 1969, in *Salix* habitats bordering the main marshes.

Date of collection	Numbers of larvae/10 traps per day		
	Collected between 0m - 10m from marsh	Collected between 12.5m - 22.5m from marsh	Collected between 0m - 22.5m from marsh
12.x	0.12 (2)[1]	0.19 (3)	0.15 (5)
18.x	0.45 (6)	0.67 (8)	0.56 (14)
26.x	0.23 (4)	0.31 (5)	0.27 (9)
9.xi	0.12 (4)	0.36 (10)	0.23 (14)
24.xi	0.15 (5)	0.33 (10)	0.30 (15)
8.xii	- (0)	- (0)	- (0)

Traps were 2.5 metres apart in each of four transects and there were 10 traps in each. [1]Figures in parentheses indicate the numbers of larvae taken from each set of traps at each collection.

0.24 larvae/10 traps per day.

One larva was extracted from samples of 22 random quadrats of 0.20 metre^2 taken in *Salix* habitats at 45^I on October 20; none were sampled from 10 quadrats in spruce forest margin and sedge meadow at 41^I on October 19.

6.2. Distribution and activity of adults, 1968 - 1969

Activity in 1968. - Adults were rare in the main study areas except for forest margins during late spring and summer. Three adults only were collected from traps in sedge meadow and *Salix* habitats, but 31 were trapped in drier habitats, mainly forest margin. Other adults were collected from under bark in September.

Activity in 1969. - Spring adults were sampled from wet bark from waterlogged hollows near forest margin. Two females from these habitats carried mature eggs on May 10. Summer adults were active in late June and probably overlapped in reproductive activity with the spring adults. Egg laying extended from early May to early August.

Adults were most active in forest clearings and sedge meadows. Between late June and early August, 66 adults were trapped in sedge meadow at 41^N, while seven were trapped in *Salix* habitats and pools and hollows adjoining the main marshes. Adults were active during the day and night. For example, on June 27 and 28 seven were trapped between 0400 and 2000 hours and five between 2000 and 0200 hours.

On September 12 and September 26, five adults and two adults respectively were found under a total of 80 boards in sedge meadow and spruce forest margin at 41^{N}.

6.3. Discussion

The low catch and distribution of larvae in 1968 was in accord with the rarity and distribution of adults. Adults and larvae were not associated with water in the dry substrate conditions of transition habitats in 1968, but were in the wet substrate conditions of 1969. The ranges of both stages expanded in 1969, and collections indicated that larvae were widespread in all wet habitat types. The high activity of larvae near the marshes in October 1969 indicates that females oviposited there.

It appears that adults of this species at George Lake are adapted to a wide range of environmental conditions, and produce a greater number of progeny in wet substrate conditions, as in 1969. Populations of *P. foveocollis* are thought not to be associated with water (Lindroth, 1961), but the local distribution of populations in some other parts of the species range may expand and contract also, according to weather changes between years.

7. *Patrobus septentrionis* Dejean

Introduction. - The species is holarctic in distribution and has the widest geographical range of the North American *Patrobus* (Darlington, 1938). There is marked geographic variation in habitat occupation. Eurasian populations of this species frequent both tundra and moist forest areas, and Icelandic ones occupy moist meadows (Larsson, 1959). North American representatives occur along the shores of standing water bodies on "more or less clayish ground with grass and *Carex* vegetation," and with the exception of those in southern Labrador, the Aleutian and Pribilof Islands do not frequent tundra (Lindroth, 1961).

Icelandic populations overwinter mainly as larvae (Larsson, 1959), and North American ones may do so also (Lindroth, 1961).

7.1. Distribution and activity in 1968 and 1969

No larvae were sampled in either year.

1968. - Few adults were trapped in June and July. Individuals were most active from the end of July to mid-August. I trapped 31 adults during the season, and 24 of these were sampled from 50 traps in Marsh I between July 24 and August 18. Four adults were trapped between 1930 and 0130 hours of a 24 hour study on August 17 and August 18. The period of reproductive activity probably coincided with the main period of activity. Adults were collected from under bark in September.

1969. - Adults were trapped from early June on to mid-August. They were most active in the sedge meadow at 41^{N}. Between late June and early August, 45 were trapped in ten E-traps at that station, while five were trapped in the same number of traps in *Salix* habitats adjoining the main marshes. Few adults were dissected, but those which were carried mature eggs in July and August. Three tenerals were trapped between late June and early July. Adults were active during the day and night. For example, on June 26 and June 27, nine adults were trapped between 2200 and 0400 hours, and four between 0700 and 2200 hours. No adults were sampled in September or October.

7.2. Discussion

Few adults and no larvae were collected in either year. It is possible that there are few or no breeding populations at George Lake, and that adults migrate in from areas outside the field station. I do not think this to be so, as adults were active and breeding in the same study areas each year, and were collected in September of 1968, apparently preparing to hibernate. Tenerals were sampled in both years and they would not have migrated into the field station easily. No adults were window trapped or observed in flight. Despite intensive sampling no larvae or pupae were found. Probably they occurred deeper in soil and so were not sampled. Thus, it is likely that populations of *P. septentrionis* are locally rare in comparison with those of other *Patrobus* species at George

Lake. In summary, populations at George Lake overwintered both as larvae and adults.

8. General discussion of comparative ecology

8.1. Taxonomic characters

A number of workers (for example, Mayr, 1963 : 59ff.) have stressed the importance in studying physiological, behavioural, and ecological characters as well as morphological ones. As a result of this field study a number of ecological characters of the *Patrobus* species at George Lake were defined (Table 19). Some of these will now be related to the taxonomy of the group. These examples will indicate that these closely related carabids are characterized by well defined mean values of both non-morphological characters and morphological ones. Other ecological characters, including life history data and certain aspects of habitat use are summarized in Table 19.

Adults of *P. stygicus* are readily distinguished from those of *P. lecontei* by for example leg colour, features of prothorax, and male genitalia (Darlington, 1938; Lindroth, 1961). Likewise, the two species are distinguished by a number of ecological characters: degree of hygrophily (and therefore habitat occupation of larvae and adults), age at which reproduction begins, maximum age at which reproduction occurs, and length of adult life (Table 19).

Patrobus longicornis Say frequents open habitats, often near the margins of rivers and lakes (Lindroth, 1961), and does not occur at George Lake. Features of habitat occupation of

Table 19. Aspects of habitat utilization and life history features of the four *Patrobus* species at George Lake.

	LARVAE			PUPAE	
	General habitats	Overwintering stage(s)	Main period of seasonal activity	Pupation	Main sites
P. stygicus	Transition to deep marsh	Larvae, Adults	July - ? Sept. - Dec.	late May - late June	Hummocks, bark in transition
P. lecontei	Transition and shallow marsh	Larvae	late Sept. - early Nov.	late May - late June	Soil, bark in transition
P. septentrionis	Transition	Larvae, Adults	late Sept. - ?	June	?
P. foveocollis	Transition, also forest clearings	Larvae Adults	Aug. - Nov.	June	?

Table 19 (Cont'd)

	TENERAL ADULTS		ADULTS		
	Teneral emergence	Habitat	Adult seasonal activity	Reproductive activity	Main oviposition sites
P. stygicus	late June - July	Transition	(1) May - ? (2) mid-June - mid-Oct.	(1) late May - ? (2) late July - mid-Aug.	*Carex* hummocks in marsh
P. lecontei	late June	Transition	mid-June - mid-Aug.	late June - mid-Aug.	*Carex* hummocks in transition
P. septentrionis	?	Transition	early June - mid-Oct.	late July - mid-Aug.	?
P. foveocollis	late June	Transition forest	(1) early May - mid-Oct. (2) late June - mid-Oct.	(1) mid-May - late June	?

Table 19 (Cont'd)

ADULTS

	Age at which reproduction begins	Maximum age at which reproduction occurs
P. stygicus	1 month (late July)	2 - 12 months
P. lecontei	1 week (late June)	2 months
P. septentrionis	?	?
P. foveocollis	?	?

(1) refers to spring adults and their larvae

(2) refers to summer adults and their larvae

P. stygicus and *P. lecontei* (Table 19) indicate that these two species are more closely related to one another than either is to *P. longicornis;* so also do morphological characters (Darlington, 1938).

The four *Patrobus* species at George Lake share a number of ecological characters. These include overwintering as larvae only or as larvae and adults, and overlap in general habitat preferences (Table 19). These and morphological characters, which Darlington (1938) and Lindroth (1961) described, indicate the close relationship of these species.

8.2. Habitat occupation and life history features

One of my objectives was to determine how closely related carabids divide up space in wet habitats during their lives. The ranges of spatial distribution of both larvae and adults of each of the *Patrobus* species differed according to time of year. The ranges were greatest during the beetles' periods of main activity between May and September, and September and November for the adults and larvae respectively (Table 19). The ranges were least prior to and just after overwintering, the periods of low activity. Habitat occupation of the carbids during periods of main and low activity are considered separately below.

During their periods of main activity, individuals of *P. stygicus, P. lecontei,* and *P. foveocollis* occurred mainly in different zones from forest clearings to the lakeside, but there

was overlap in general habitat occupation of all species. Larvae and adults of *P. foveocollis* predominated in drier parts of the transition zone, such as forest clearings. Those of *P. lecontei* occupied mainly the wetter parts of this zone, chiefly sedge meadow and *Salix* habitats, while individuals of *P. stygicus* ranged into the wettest habitats, that is those in deep marsh. Adults of *P. septentrionis* appeared to be as hygrophilous as *P. lecontei* but were locally rare at George Lake and occurred chiefly in sedge meadows. Individuals of all four species were found in sedge meadows, also *Salix* habitats, but only *P. lecontei* and *P. stygicus* adults frequented large pools where there was little or no sedge growth.

Habitat occupation of adults differed prior to and during their periods of reproductive activity. Breeding spring adults of *P. stygicus* and summer adults of *P. lecontei* occupied the same general habitats in late June and July, namely pools in sedge meadows, *Salix* habitats, and to a lesser extent, shallow marsh. Summer adults of *P. stygicus* dispersed from these habitats into deep marsh in late July and August.

The range of spatial distribution of larvae and adults decreased as they dispersed to drier habitats such as *Salix* ones, banks of pools, and forest margin prior to overwintering. No adults of *P. lecontei* were found to survive past their breeding

season, but adults of the other three species tended to occur together in fall and winter. Third instar larvae overwintered and were aggregated in spring. There were differences among late third instar larvae and pupae with respect to vertical distribution above and below soil surface. Larvae and pupae of *P. stygicus* were mainly in hummocks and bark above soil, while those of *P. lecontei* were found above and below soil. Despite intensive sampling late third instar larvae of *P. foveocollis* were sampled rarely and no larvae of *P. septentrionis* were found. Probably, larvae of these latter two species occurred deeper in soil and so were not sampled.

It is evident from the above data that the different habitat preferences of the *Patrobus* species at George Lake, particularly during their main periods of activity, were reflected mainly in their various horizontal distributions. Seasonal differences in habitat occupation have also been observed for adults of some marsh carabids in Britain. Dawson (1965) and Murdoch (1963) found clear differences in summer habitats between a number of congeneric marsh carabids, but observed that they overwintered together in drier habitats. It may be that adults of hygrophilous carabids normally aggregate together in dry overwintering quarters, such as bark in forest margin, but disperse to different spring and summer habitats according to their respective responses to water. Thus congeneric carabids for example, such as those of the *Patrobus*

species at George Lake, come to occupy different habitats during their main breeding seasons.

Some life history features will now be considered as adaptations to wet habitats (Cole, 1954). Differences in habitat occupation of the beetles will be related to these adaptations. The life history features considered in this study were stage of overwintering, age at which reproduction begins, and maximum age at which reproduction occurs.

Cole (1954) proposed that "a change in life history which would add one to the litter size would be more likely to occur than a change permitting repeated reproduction which in many cases would necessitate adjustments to survive several seasons of dormancy." Murdoch (1963, 1966*a*, 1966*b*) found that individuals of some marsh carabids he studied overwintered to a second breeding season and on the basis of this observation he took exception to Cole's suggestion. He proposed that poor breeding in one season was compensated for by high adult survival from the end of one breeding season to the beginning of the next. It is well known that some carabids of forest and open habitats survive to breed in their second season (for example, Van der Drift, 1951; Schøtz - Christensen, 1961). Holgate (1967) pointed out that Cole's model was entirely deterministic. Pielou (1969 : 8) described a deterministic process of population growth as one which "assumes not that an organism may reproduce but that in fact it does reproduce with absolute certainty." Holgate (1967) used a stochastic model, that is, one

in which chance mechanisms are incorporated, and found that incidence of random extinction of isolated populations are reduced by individuals surviving to a second breeding season. Thus, his model supported the field and experimental data of Murdoch (1966*b*).

It is worth noting here that the majority of hygrophilous carabids of both Europe and North America overwinter as adults, and only a very few as larvae (Lindroth, 1949, 1963; Murdoch, 1967). Murdoch (1967) suggested that eggs and larvae are not so well adapted as adults to withstand rising water levels in fall and winter in Europe. Whatever the selective pressures are that produce and maintain the life history pattern of adult overwinterers of most North American hygrophilous carabids, it would appear that hygrophilous carabids with different life history patterns such as the *Patrobus* species must have peculiar adaptations to wet habitats.

The advantages to populations of *P. stygicus* and *P. septentrionis* in overwintering as both larvae and adults are probably as follows. If the spring adults are low or are affected by unfavorable environmental conditions, the first year summer adults will add to stability. Water from the snow melt ensures that favourable conditions exist into June of most years, for the spring adults. If unfavourable conditions persist throughout the season a greater number of the summer *P. stygicus*, for example, may overwinter as sexually immature rather than breeding during their first year.

Populations of *P. lecontei* overwinter as larvae only. If

overwintering in two stages contributes to population stability in *P. stygicus*, *P. lecontei* must have other mechanisms to achieve the same end. It would appear that populations of this species can increase their botic potential only by increasing the litter size. Adults of *P. lecontei* are characterized by a short pre-reproductive period and a short life, while those of *P. stygicus* have a long pre-reproductive period and a longer life. Other workers (e.g. Murphy, 1968 with fish; Dingle, 1968 with a bug; and Tinkle *et al.*, 1970 with lizards) have found that species with a short period of sexual development and short adult life have high fecundity. Possibly, *P. lecontei* also has high fecundity and benefits from early reproduction and maximizes population growth by increasing the rate of reproduction. Also, the sexual development of adults of this species is possibly less affected by weather for example, because of their early reproduction. On the other hand, as noted above, *P. stygicus* achieves population stability by the survival of adults to a second season.

Dingle (1968) pointed out that species which delay reproduction face increased hazards in pre-reproductive life and lower reproductive values. However, he indicated that depressed reproduction results in longer life and may buffer population fluctuations. Regarding the latter, Murdoch (1966*a*,*b*) proposed that poor breeding in one season was compensated for by high adult survival from the end of one breeding season to the beginning of the next. The difference in age composition of adults of *P. stygicus*

within and between years according to differences in water levels (4.2.2.2.), indicate consequent effects of weather on species such as *P. stygicus* with delayed reproduction.

Thus, it appears that *P. lecontei* and *P. stygicus* evolved different life history features in response to different evolutionary pressures generated by their different habitat occupations.

8.3. Phylogeny

The evolutionary interpretation of life history features and other ecological characters are based on Darlington's hypothesis of the phylogeny of the *Patrobus* species. He used morphological and zoogeographical characters. He wrote that the genus *Patrobus* probably originated in Asia and that the ancestors of the present day North American species migrated into the continent through the north at three times.

He proposed that stock to arrive first was temperate, and that it divided into a boreal line (proto *fossifrons-lecontei*) and a temperate line (proto *longicornis*) which gave rise to *P. longicornis*. The former stock "then divided into a western species (proto *fossifrons*, probably west of the rockies) and an eastern species (proto *lecontei*, probably east of the rockies)" (Darlington, 1938). Later, proto *fossifrons* entered the range of *P. lecontei* by migrating eastward. The eastern and western populations of proto *fossifrons* became isolated and differentiated, giving rise to the ancestors of present day populations of *P. fossifrons* and

P. stygicus. Darlington (1938) included these four species in the same subgenus, named *Neopatrobus*.

The morphological changes (for example, the male genitalia, pronotum, and leg size and colour) which took place during the evolution of the *Neopatrobus* group proceeded from a primitive extreme in *P. longicornis* to the derived extreme in *P. stygicus*. The series of characters can be described as a morphocline (Maslin, 1952).

The ecological trends of the ancestors of this first *Patrobus* stock that reached North America may be as follows. *Patrobus longicornis* Say frequent riparian habitats mainly, but appears not to be directly dependent on water. This species appears to be the most primitive one of *Neopatrobus* (Darlington, 1938) and so the ancestors of this line may have frequented such riparian habitats.

The *lecontei-fossifrons-stygicus* line diverged from temperate habitats into wet boreal ones, with the proto-*fossifrons-stygicus* stock becoming the most hygrophilous. The ancestors of *P. fossifrons* and *P. stygicus* dispersed into wetter habitats (marsh) than those frequented by the ancestors of *P. lecontei*. Today this is reflected in the segregation of *P. stygicus* summer adults from *P. lecontei* adults during the breeding season of the former.

This change in habitat preferenda in the evolutionary history can be described in terms of the ecocline. This cline proceeds from the primitive extreme in *P. longicornis* which tends to be riparian, to *P. lecontei* the largely transition zone dweller, to

the derived extreme in *P. stygicus* which is a transition zone and marsh dweller. Thus, this ecocline extends from the primitive condition of least hygrophily to that of most hygrophily. It runs in the same direction as the morphoclines identified by Darlington (1938).

Patrobus foveocollis and *P. septentrionis* migrated to North America later than the *Neopatrobus* stock (Darlington, 1938). *Patrobus foveocollis* remained in drier boreal habitats than those entered by the *Neopatrobus* stock. The *P. septentrionis* stock converged ecologically with this group as they dispersed into wet boreal habitats. Both *P. foveocollis* and *P. septentrionis* retained the primitive condition of overwintering as larvae and adults.

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